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Spatial scale in games of habitat selection, patch use, and sympatric speciation

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Most organisms live in heterogeneous environments. Yet we know little about how variations in scales of heterogeneity influence decisions on patch use and habitat selection, and how they impact spatial distribution and evolution. In particular, we need to know whether the choice of habitats and patches emerges from a hierarchy of decisions, whether resource consumption correlates closely with space use, and whether different types of individuals are associated with patterns of spatial distribution. I address these knowledge gaps with field experiments that manipulated the risk and quality of foraging patches exploited by male meadow voles. I used clear versus wooden covers to create risky versus safe foraging sites and added supplemental food to create rich versus poor habitats. I assessed whether the resources harvested from each tray matched its frequency of use by groups of voles expressing different temperament scores. Habitat and patch use did not fit a simple hierarchy of decisions because animals merged space use and foraging speed in a sophisticated strategy of risk management. Giving-up densities mirrored activity densities at the scale of safe versus risky patches but not at the scale of safe versus risky or rich versus poor habitats. Voles tended to prefer one habitat over another for reasons independent of the experimental manipulations. Groups of voles with different temperament scores were not linked to foraging types but were linked to habitat preference. The bias in habitat use by different behavioural types provides a potential mechanism for the evolutionary divergence of populations occupying different habitats.

Keywords: evolutionary games; giving-up density; habitat selection; patch use; spatial scale; vole

Introduction

Best strategies of patch use and habitat selection are typically modelled as fitness-maximizing solutions to evolutionary games played at different spatial scales. Pay-offs from patch use emerge from the marginal (often energetic) value obtained from patches differing in harvest costs, predation risk, and missed opportunities of engaging in alternative activities (Brown 1988). Pay-offs from strategies of habitat selection emerge from the relationships between fitness and the densities of individuals living in (often discrete) habitats (Fretwell & Lucas 1969; Rosenzweig 1981; Morris 1988; Brown 1990; Vincent & Brown 2005; Křivan et al. 2008; Cressman & Křivan 2010). Each cost in the foraging game will also depend on density, so the best patch-use strategy should, at some appropriate scale, predict habitat selection (Morris 2011). The prediction has been confirmed in meadow voles where invader-strategy landscapes (Apaloo et al. 2009) built from mean quitting harvest rates (QHRs) and GUDs project the best strategy of habitat selection (Morris 2014). But we do not yet know whether a similar correspondence might also exist at individual patches accessed by many individuals. I address this shortcoming with experiments on meadow voles. The experiments were designed to answer three deceptively simple questions: (1) Does the number of foragers accessing a single resource patch predict its giving-up density? (2) Do different types of foragers visit safe versus risky patches? (3) Do the answers to 1 and 2 depend on the spatial scale of risk and safety?

The answers have potentially far-reaching implications. Habitat selection is often modelled as a hierarchical process (Johnson 1980). Decisions at one scale of resolution, such as home ranges, are assumed to influence the use of foraging patches and are cumulated into larger scale patterns (e.g., Rettie & Messier 2000; McLoughlin et al. 2004). This formulation, although appropriate for describing patterns, fails to include the interplay among scales that determine patterns (Orians & Wittenberger 1991). It also fails to incorporate other types of feedbacks between population density and individuals that influence habitat choice and patch use (e.g., Stamps 1987, 1988; Green & Stamps 2001; Chalfoun & Schmidt 2013). Individuals might often base their decisions on various forms of public information (Doligez et al. 2002; Danchin et al. 2004) or be constrained in patch and habitat selection by early development (e.g., Wecker 1963; Davis & Stamps 2004). Habitat selection can similarly be constrained by the decisions of, and value of living with, other individuals (e.g., Courchamp et al. 2008; Meldrum & Ruckstuhl 2009).

Habitat selection also represents a common mechanism of risk management (Brown & Kotler 2004) and one of the more viable options leading to sympatric ecological speciation (Rosenzweig 1978, 1995; Rauscher 1984; Rice 1987; Jaenike & Holt 1991; Edelaar & Bolnick 2012). Ecological speciation is enhanced if switching from using one habitat to another entails cost, or if individuals differ in their efficiencies at harvesting resources from different habitats (Nosil 2012). Whether the ensuing speciation is

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legitimately called sympatric will depend on the scale of patches and the scale at which different types of individuals use those patches. Bold versus shy personalities (e.g., Sih et al. 2014), for example, can emerge when risk and reward co-vary: positive feedback loops yield either bold risk-taking individuals in a high energetic state or shy conservative individuals retaining a low energetic state (Luttbeg & Sih 2010). Foraging decisions by all types of individuals also depend on, and reveal, the spatial pattern of predation risk (e.g., Lima & Dill 1990; Lima & Bednekoff 1999; Laundré et al. 2001, 2010; Druce et al. 2006) that varies with the spatial scale of safe and risky habitats.

Keeping these points in mind, I designed experiments to (1) evaluate scale-dependent preferences for habitat and foraging sites; (2) explore whether putative differences among individuals alter those choices when animals are forced to experience different scales of safety and risk; and (3) learn whether animals exhibit similar responses when habitats differ in resource supply.

Materials and methods

Common methods

I manipulated predation risk and resource densities for meadow voles (*Microtus pennsylvanicus*) in two separated pairs (referred hereafter as 1 and 2, and 3 and 4, respectively) of 25- × 25-m vole-proof metal field enclosures in northern Ontario, Canada (Lakehead University Habitron, 48°19′49″ N, 89°47′27″ W; NAD 83) during June, July, and August 2014. Each enclosure contained young red pine (*Pinus resinosa*) ~4–5 m tall with an understory of mixed grasses and forbs (Halliday et al. 2014; Morris & MacEachern 2010). My team and I placed two pairs (safe and risky) of plastic "bell-pot" foraging trays (40 cm diameter) in the shade of a red pine tree at diagonal corners in each enclosure. We protected trays from wind and rain with a 60 cm × 60 cm × 14 cm wooden frame covered either by a clear polyethylene sheet (open = risky) or plywood (cover = safe). Voles consistently spend more time, and forage more intensely, in covered than in open trays (e.g., Morris 2014). We mixed 8 g of whole oats in 1.5 L of sieved silica sand, and poured the mixture into the foraging trays at 12:00 h one day after voles were released on 8 June and collected the trays 22 h later. We sieved the sand, cleaned the sample, and weighed the remaining oats to determine each tray's giving-up density (GUD), and recharged the trays with oats. We repeated this regimen daily for the full duration of the first experiment (manipulating risk; 13 June until 14 July) and four days weekly for the second experiment (manipulating food; 8 versus 16 g oats; 4–29 August).

We placed a "blinded" RFID antenna (Vantro Systems, Burnsville, MN, USA) that automatically recorded the entry and departure times of marked voles under each foraging tray of one pair of adjacent enclosures, at the single 9.25-cm gate between those enclosures, and one along each of the adjoining walls (total of 12 antennae). We used these data to determine the number, identity, and foraging times of voles recorded by each antenna (and respective enclosure). There were no antennae in the second pair of enclosures.

Beginning in late May, I implanted 30 naïve adult male meadow voles with passive radio-frequency identification transponders (RFID, Trovan 100) that were reliably detected by the antennae. These animals were captured either elsewhere in the Habitron or nearby in natural habitat where they lived under similar conditions and should thus have been in similar physiological, reproductive, and behavioural states. I did not include females in order to avoid inevitable changes in density over the 10-week duration of the experiments. My purpose was to assess habitat and patch use under experimental conditions altering the scale of safety and risk, not differences between sexes or with changes in the density and composition of the population.

My field team and I released the voles in other field enclosures prior to the experiments, so they would become accustomed to living within the Habitron. We recaptured the animals and used a modified hole-board open-field arena to assess each animal's temperament traits (e.g., Martin & Réale 2007, details in Morris et al. 2016; these observations were blinded by body size and allocation of subject animals to enclosures and treatments) before placing six randomly chosen individuals in each of the experimental enclosures on 8 June. We allowed the animals to habituate to their new surroundings and foraging opportunities for three days before opening the gate between one pair of enclosures (1 → 2) on 11 June. Animals could not move between enclosures in the second pair (3 and 4, control on movement, the temporal sequence of manipulations is illustrated in the online supplement). We allowed the animals a further three days to acclimate. We collected GUDs and RFID records during the acclimation period but I analyse only data collected after the experiments began on 13 June.

Experiment 1: manipulating the scale of risky patches (13 June–14 July 2014)

We used the pattern of open versus covered foraging patches to manipulate risk at two spatial scales corresponding, respectively, with individual foraging stations and enclosures. We placed one open and one covered foraging tray at each of the two locations (arbitrarily called "A" and "B") in each of two diagonal stations within an enclosure (four trays total). Voles using each of those stations were thus exposed to either a safe or risky foraging opportunity. We then moved covers such that there were only open stations in one enclosure, and only covered stations in the other, to produce relatively safe versus risky enclosures.

The experiment consisted of four temporal sequences (= treatments): first control (all stations with one open and one covered foraging tray); first risk period (one enclosure with all open and the other with all covered trays); crossover risk period (reversal of the first risk period by moving covers such that the 'open' enclosure

became 'covered' and vice versa); second control (all stations again with one open and one covered tray). This sequence was followed by a second complete sequence (replicate) after we live-captured all animals and exchanged them between the open-gate and closed-gate pairs of enclosures (animals from enclosures 1 and 2 randomized between enclosures 3 and 4 and vice versa on 25–27 June; 35 Longworth live traps placed in each enclosure; one animal was not recaptured, so I replaced it with one of the "spare" animals marked earlier). Animals that were monitored by RFID antennae and free to move between enclosures in the first sequence were not monitored by RFID antennae or free to move in the second sequence and vice versa (an illustrated guide to this design is provided in the online supplement). The design ensured that all animals experienced all possible treatments. The gate between enclosures 1 and 2 was closed at the end of the experiment.

Experiment 2: manipulating rich patches (4–29 August 2014)

This experiment also used replicated temporal sequences with most of the same animals assigned to experiment 1. We live-trapped animals in the experimental enclosures on 29 and 30 July with the same effort that we employed in experiment 1. Seven animals were not recaptured, so I replaced them with seven previously tagged males of similar size (again with initial densities of six animals in each enclosure, some attrition between experiments was expected because the enclosures were not protected from rodent predators). I reopened the gate between enclosures 1 and 2 after trapping was completed on 30 July. We allowed the animals to acclimate until 4 August when we placed 8 g of oats in each open and covered tray at the stations in one randomly assigned enclosure of each pair and 16 g of oats in each open and covered tray in the other two enclosures. The design thus manipulated resource quality only at the scale of enclosures while maintaining the scale of safety (cover) versus risk (open) at individual stations. We maintained this manipulation for four consecutive days, removed trays for three days, then crossed it over by reversing the treatments for a further four days (the previously "poor" 8 g enclosure became rich (16 g of oats), while the previously "rich" 16 g enclosure became poor (8 g oats)). We then live-trapped and exchanged voles between the pairs of enclosures and "repeated" the experiment (again ensuring that all animals experienced all possible treatments; this design is also illustrated in the online supplement).

Caveats

Animal personalities require repeated assessments on individuals in order to reveal consistent behaviours that are stable in time, space, and context (Martin & Réale 2007; Dingemanse & Dochtermann 2013; Dall & Griffith 2014). Assigning the variation from single observations to represent different behavioural states or personalities would be misleading if the behaviours are not repeatable. My purpose in measuring temperament was different. I simply aimed to use the covariation among traits to search for mean differences among animals using different strategies of patch and habitat use. Restricting the study to males yielded animals in an inherently stable state known to induce time-consistent behaviour (Wolf & Weissing 2010). Although I do not know what an animal's emergent personality might have been, the context and assessment of behaviour were constant for each individual and should thus be reliable indicators of differences among them. I thus assume that my measures of temperament represent differences among individuals that are maintained through time (Dingemanse et al. 2010) but not that they uniquely identify each individual's personality. This assumption implies that individuals can adjust their habitat use according to my initial assignments of differences in temperament, and that those adjustments exceed plasticity in the same traits induced by changes in state or surroundings (e.g., Stamps & Groothuis 2010; Wolf & Weissing 2010; Stamps 2016).

Restrictions, hypotheses, and expectations

The risk experiment was designed to enable comparisons of treatments with both temporal and spatial (free to move or limited to a single enclosure) controls. GUDs were consistently lower in the paired enclosures with closed gates (3 and 4) than they were in the pair with open gates (1 and 2). I attribute the difference in GUDs to differences between enclosures in their innate quality (animals were randomly assigned so they could not carry over a condition bias into the experiment) and thus limit analyses to the two enclosures for which I possess both GUDs and RFID data.

In order to answer question 1 (*Does the number of foragers accessing a single resource patch predict its giving-up density?*), I proceeded with the working hypothesis (1) that the GUD should be inversely proportional to the number of foraging visits voles made to a tray of a given type (safe or risky; rich or poor). More visits yield a lower GUD. This hypothesis would be true, for example, if activity density is a reliable indicator of patch preference and quality. If individuals are free to choose any patch or habitat available to them, then individuals should most often choose the patch or habitat of the highest quality. We should thus also expect (2) more foraging visits in the safe habitat relative to the risky one as well as (3) more visits to the rich 16-g habitat compared with the poorer 8-g one. These differences should be reflected in the harvest curves associated with each treatment. And if foraging visits and GUDs are indeed complementary, then (4) both variables should reveal similar patterns of variation between safe versus risky sites and rich versus poor sites.

In order to answer question 2 (*Do different types of foragers visit safe versus risky patches?*), I expected that if groups of voles differ in behaviour, then different groups should (5) express different foraging repertoires, and if they differ in temperament traits, then different behaviourally identified groups of individuals should (6) belong to different foraging classes and, (7) be associated with habitats that differ in risk and quality.

I answered question 3 (*Do the answers to 1 and 2 depend on the spatial scale of risk and safety?*) by comparing patterns at the patch versus habitat scales.

Analysis

Risk experiment

I restricted analysis of the risk experiment to the two paired enclosures in which I recorded animal visits with RFID antennae. I discarded the first day of the two control periods to eliminate carryover effects and to also create a balanced statistical design. I combined data for the two time sequences (two groups of animals) because animals were randomly allocated among enclosures at the start of the experiment, all animals experienced the treatments in the same order, all comparisons use data paired by tray and time that control for any differences between groups of animals, and because my primary interest is related to evaluating the correspondence between activity density and GUD. I thus tested predictions (1) and (2) (GUD is inversely proportional to foraging visits; more visits to the safe habitat) with a saturated repeated-measures mixed model that explored the main effects of tray (A vs. B), enclosure (1 vs. 2), treatment (2 control periods, 2 risky periods), and their interactions (dependent variable = number of vole visits to the patch, number of visits at a tray repeated for each 22-h foraging assessment, random effect = station). I used an identical analysis with the data on GUDs in order to evaluate whether the pattern of significance was identical between the two patch-use measures (prediction (4)).

Food experiment

I used the same form of mixed model to analyse data from the food experiment (to test prediction (4); more visits to the rich habitat). I moved the two RFID antennae along the walls in enclosures 1 and 2 to a similar location in enclosures 3 and 4 after exchanging animals between enclosures. I did so in order to verify that no animals in those enclosures had escaped capture. Unfortunately, some voles were able to crawl up the attached cables and made their way back into enclosures 1 and 2. Foraging by these animals destroyed the independence between the two "exchanges", so I analysed only the data from the first replicate of this experiment.

Temperament scores

I used the scores from two "temperament Principal Components" (PCs) calculated by Morris et al. (2016) to quantify the behaviour of each vole. The scores summarized nine open-field box variables measured on a much larger sample (190) of voles, including all of those used in this experiment. The first component represented an activity and boldness cline, while the second portrayed stress and vigilance (Morris et al. 2016). I then estimated the mean "temperament trait score" (for each PC) of all animals visiting a single station during one 22-h foraging period (one score for each animal). I reasoned that a potential role for habitat in sympatric speciation would be revealed if the mean PC scores differed between enclosures (prediction (7), different behavioural groups in each habitat type, mixed model, station = random effect). All mixed models were analysed with SPSS Version 22 (effective degrees of freedom estimated with Satterthwaite's approximation).

Harvest curves

I estimated harvest curves from the RFID and GUD data with quadratic regressions describing the amount of oats eaten (the difference between the initial mass of oats and the GUD) during the total time spent by all foragers exploiting a patch (Morris 2014). Quadratic models of harvest curves are free of biological assumptions and provide an excellent fit ($R^2 > 0.9$) to resource harvest in depleting patches (Morris 2014).

Foraging class

I used the derivative of the harvest curves (Morris 2014) to calculate, for each 22-h foraging period, the expected QHR achieved by each vole when it left the covered foraging patch for the last time ($N = 466$, risk experiment only, all with 8 g of whole oats). I used these data to calculate the mean expected QHR achieved from the total number of estimates (5–44) acquired by each vole. I generated 1000 independent random samples (each sample without replacement, MINITAB 17) from the 466 estimated QHRs. The number of observations in each random sample was the same as the number of observations used to estimate each vole's mean QHR. I calculated the 95% confidence intervals in each group of 1000 random samples and evaluated (prediction (5); voles can be categorized by differences in foraging repertoires) whether the mean expected QHR of each rodent was within ("average foraging class"), less than ("late foraging class") or greater than ("early foraging class") the confidence interval. I completed the analysis by evaluating whether groups of voles with different temperament trait scores comprised the three alternative foraging classes (prediction (6), groups with different temperaments belong to different foraging classes, GLM on PC scores across foraging classes, enclosure, and experiment (risk vs. food addition, SPSS Version 22).

Results

Risk experiment

Voles preferred the "B" tray over the "A" tray (Figure 1(F)), but primarily because "B" was under the safety of cover during the two control periods (tray × treatment interaction; $F_{3,33.4} = 26.2$, $P < 0.001$, Table 1, Figure 1(B). GUDs, as expected, showed the "opposite" pattern being the highest in the underused "A" tray and the lowest in tray "B" (Figure 1(E)), and especially so during the controls ($F_{3,27.2} = 172.5$, $P < 0.001$, Table 1, Figure 1(A); prediction (1) confirmed at the scale of individual patches – the GUD was inversely proportional to the

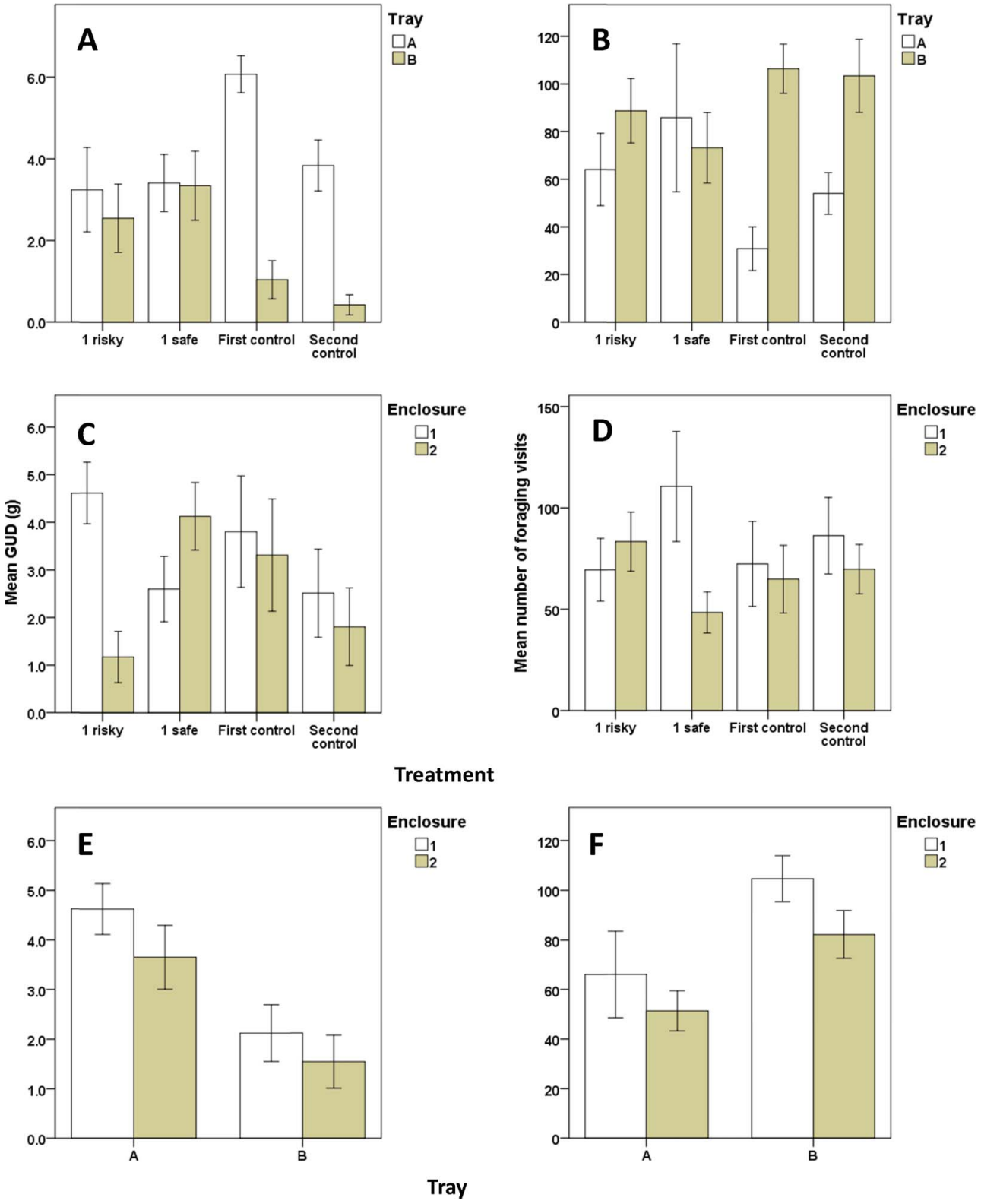

Figure 1. Illustrations of the effects of treatment (risky vs. safe habitat), tray location (A vs. B), and enclosure (1 vs. 2) on two measures of vole foraging behaviour. Panels on the left correspond with mean GUDs, those on the right with the numbers of visits. Vertical lines represent 95% confidence intervals.

number of visits by foraging voles). The number of foraging visits in an enclosure by voles with access to both depended on treatment (enclosure × treatment interaction; $F_{3,33.4} = 12.8$, $P < 0.001$, Table 1). Voles generally preferred enclosure 1 over 2 especially when 1 was safe, but reversed their preference when it was risky (Figure 1(D); prediction (2) confirmed – voles preferentially used the safe habitat). But although GUDs yielded the same significant enclosure × treatment interaction (Table 1), the pattern was different. GUDs were higher when the number of visits was low in a risky enclosure but they did not mirror the pattern of visitations during the control periods (compare the

Table 1. Results of saturated mixed models assessing the effects of tray (A vs. B), enclosure (1 vs. 2), and treatment (safe vs. risky) on the number of foraging visits and giving-up densities of male meadow voles in northern Ontario, Canada. Station treated as a random effect. Denominator degrees of freedom estimated with Satterthwaite's approximation. Bold lettering indicates statistically significant ($P < 0.05$) results.

Source	df	*F*-ratio	Significance
	Number of visits		
Intercept	1, 39.8	**1473.6**	**<0.001**
Tray	1, 39.8	**86.8**	**<0.001**
Enclosure	1, 39.9	**24.7**	**<0.001**
Treatment	3, 33.4	**6.8**	**0.001**
Tray × Enclosure	1, 39.8	2.4	0.13
Tray × Treatment	3, 33.4	**26.2**	**<0.001**
Enclosure × Treatment	3, 33.4	**12.8**	**<0.001**
Tray × Enclosure × Treatment	3, 33.4	**7.6**	**0.001**
	Giving-up density		
Intercept	1, 38.5	**2238.9**	**<0.001**
Tray	1, 38.5	**462.7**	**<0.001**
Enclosure	1, 38.5	**27.9**	**<0.001**
Treatment	3, 27.2	**30.4**	**<0.001**
Tray × Enclosure	1, 38.5	**6.5**	**0.015**
Tray × Treatment	3, 27.2	**172.5**	**<0.001**
Enclosure × Treatment	3, 27.2	**73.2**	**<0.001**
Tray × Enclosure × Treatment	3, 27.2	1.2	0.343

relative heights of bars in Figure 1(C) with those in Figure 1(D); prediction (4) rejected – the patterns revealed by GUDs were not redundant with those revealed by activity density).

Food experiment

Voles again showed a clear preference for safe (more visits under cover) over risky (open) trays ($F_{1,20.2} = 42.2$, $P < 0.001$, Table 2, Figure 2(F)) that

Table 2. Results of saturated mixed models assessing the effects of tray (A vs. B), enclosure (1 vs. 2), and treatment (high vs. low food) on the number of foraging visits and giving-up densities of male meadow voles in northern Ontario, Canada. Station treated as a random effect. Denominator degrees of freedom estimated with Satterthwaite's approximation are 1 and 20.191 for visits and 1 and 17.735 for giving-up densities, respectively. Bold lettering indicates statistically significant ($P < 0.05$) results.

Source	F-ratio	Significance
	Number of visits	
Intercept	**464.54**	**<0.001**
Tray	**42.19**	**<0.001**
Enclosure	0.24	0.88
Treatment	**5.40**	**0.03**
Tray × Enclosure	0.75	0.40
Tray × Treatment	1.73	0.20
Enclosure × Treatment	3.97	0.06
Tray × Enclosure × Treatment	3.61	0.07
	Giving-up density	
Intercept	**411.66**	**<0.001**
Tray	**190.30**	**<0.001**
Enclosure	1.44	0.25
Treatment	3.18	0.09
Tray × Enclosure	0.20	0.66
Tray × Treatment	**7.22**	**0.02**
Enclosure × Treatment	**126.27**	**<0.001**
Tray × Enclosure × Treatment	**65.14**	**<0.001**

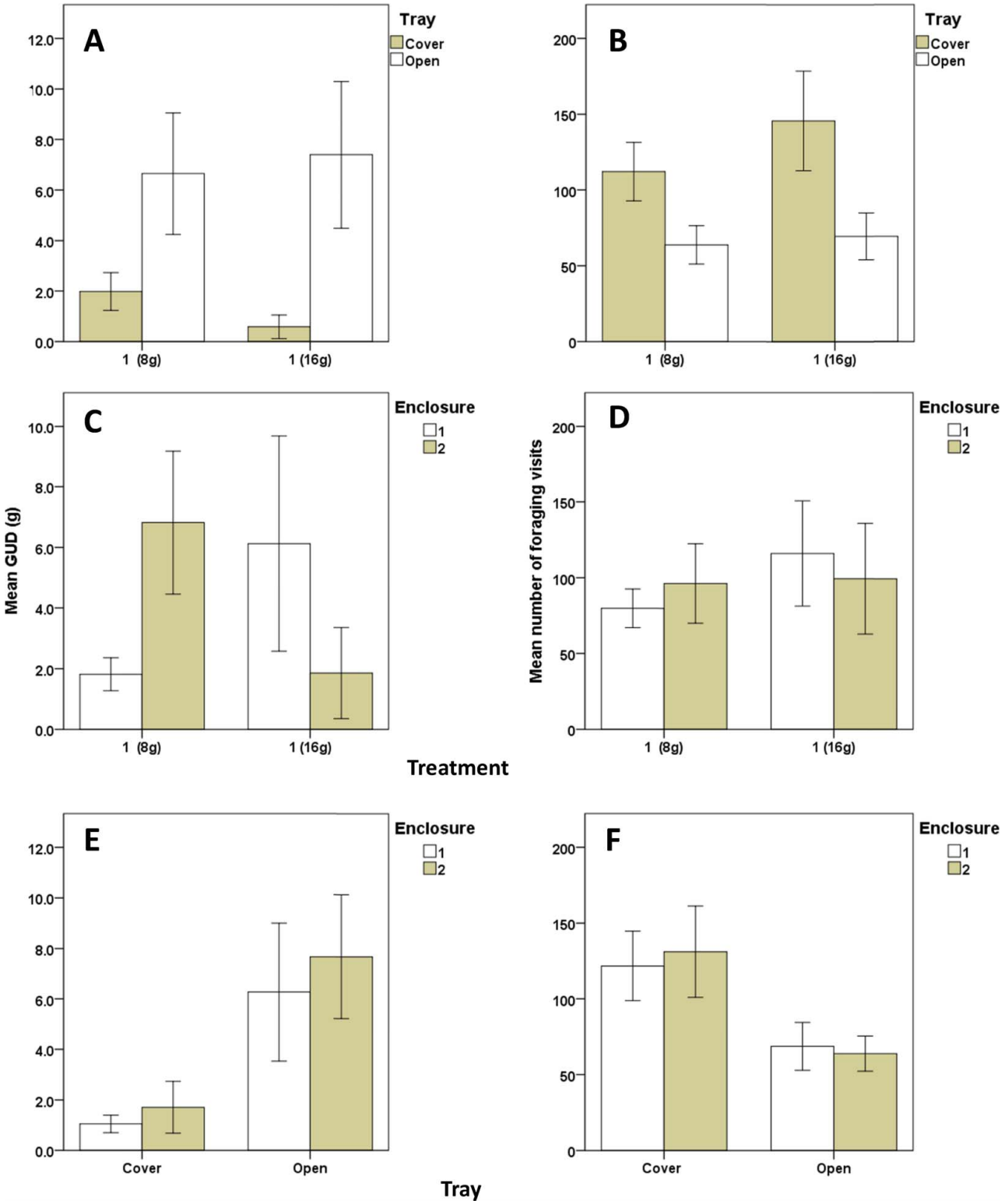

Figure 2. Illustrations of the effects of treatment (rich vs. poor habitat in enclosure 1), tray (cover vs. open), and enclosure (1 vs, 2) on two measures of vole foraging behaviour. Panels on the left correspond with mean GUDs, those on the right with the numbers of visits. Vertical lines represent 95% confidence intervals.

was reflected as the mirror image in GUDs (GUD lowest in safe trays; $F_{1,17.7} = 190.3$, $P < 0.001$, Table 2, compare Figure 2(B) with Figure 2(A)). The result reconfirms prediction (1) that the GUD was inversely proportional to the number of foraging visits. Voles also preferred (prediction (3)) the rich over poor habitat ($F_{1,20.2} = 5.4$, $P = 0.03$, Table 2, Figure 2(B) and 2(D)). That preference appeared to depend on which enclosure was considered, as well as treatment and enclosure differences among trays, but both effects were weak ($0.06 \leq P \leq 0.07$; Table 2). Patterns in GUD included an additional tray × treatment interaction that was not

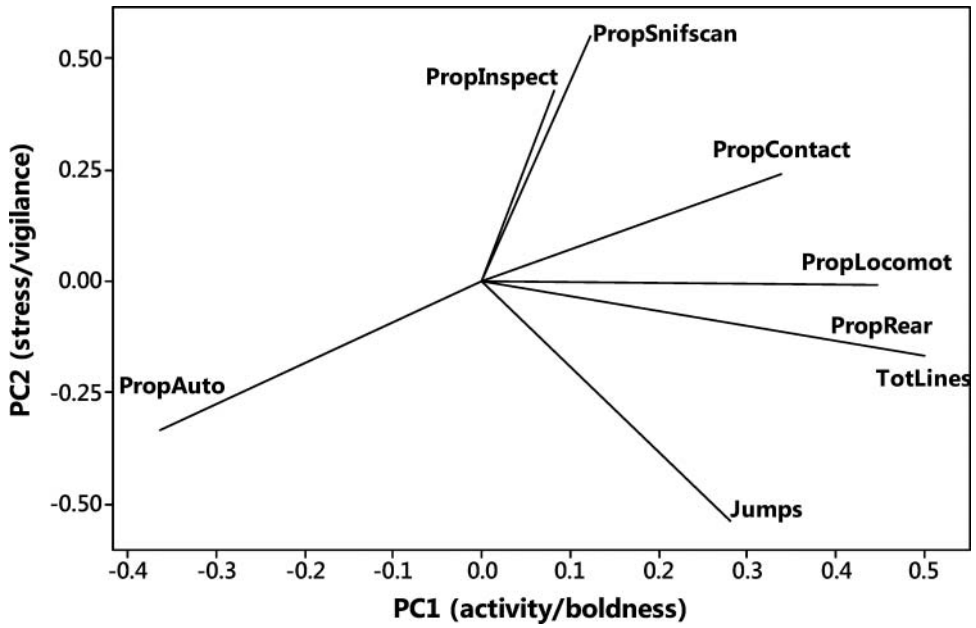

Figure 3. Principal component bi-plot summarizing personality traits extracted from open-field tests on meadow voles in northern Ontario, Canada. PropAuto, proportion of time spent grooming; PropInspect, proportion of time spent inspecting holes; PropSnifscan, proportion of time spent sniffing and scanning surroundings; PropContact, proportion of time in contact with a novel object; PropLocomot, proportion of time spent moving; PropRear, proportion of time standing on hind legs; TotLines, the number of lines crossed; Jumps, the number of jumps. Projections for PropRear and TotLines overlap one another. All data were recorded during two five-minute intervals. Complete descriptions are in Morris et al. (2016).

significant for activity density. Although GUDs were the lowest in safe trays, the difference depended strongly on treatment and enclosure (two-way interactions: tray and treatment, $F_{1,17.7} = 7.2$, $P = 0.015$; enclosure and treatment, $F_{1,17.7} = 126.3$, $P < 0.001$; three-way interaction, $F_{1,17.7} = 65.1$, $P < 0.001$; Table 2, Figure 2(A), 2(C), and 2(E); prediction (4) rejected – the patterns revealed by GUDs were again not identical to those revealed by activity density).

Temperament scores

Two axes accounted for 55% of the variation in open-field traits (Figure 3). The primary axis identified a cline of behaviour representing activity and boldness. Low scores were obtained from relatively inactive animals that spent much of their time grooming; high scores the opposite. The secondary axis corresponded with a gradient of vigilance and stress. Animals with high scores spent much of their time scanning their environment. Animals with low scores mixed attempts to escape (jumps) with grooming behaviour.

The mean PC scores were different among enclosures in five of six comparisons (all mixed models with $P \leq 0.05$ except replicate 1 of the risk experiment; $F_{1,32.4} = 2.2$, $P = 0.14$, Figure 4), but not in a way that easily corresponded with risk and quality. Prediction (4) was thus partially confirmed – groups of animals possessing different temperaments were associated with habitat, but not with treatment differences in risk and quality. The group of animals with low scores on both PCs (relatively inactive, shy, stressed animals) preferred enclosure 1; the group with higher scores (active, bold, and vigilant) preferred enclosure 2 (Figure 4).

Harvest curves

Harvest curves varied between safe and risky foraging trays, and most dramatically when both trays were rich (16 g; Figure 5). The differences in harvest curves appear to account, at least partially, for the lack of correspondence between activity densities and GUDs. I explored this possibility with quadratic regressions of the cumulative time spent in safe and risky trays versus the total number of visits made to those trays (regressions forced through the origin; Figure 6). The number of hours spent foraging tended to level off as the number of visits increased (quadratic regressions always improved on linear models) but the relationships varied between safe and risky patches, and between rich and poor treatments.

Foraging class

Vole foraging behaviour was represented by three more or less equal foraging classes (prediction (5) confirmed – different groups of animals expressed different foraging repertoires). Mean QHRs of nine voles were less than expected (late foragers), QHRs of eight voles were greater than expected (rapid foragers), and seven were not different from random (average foragers).

Effects of temperament on foraging behaviour

There was no difference in PC scores among the three more or less discrete foraging classes ($F_{4,34} = 1.16$, $P = 3.8$; GLM); reject prediction (5) – groups of animals with different temperaments do not represent different foraging classes).

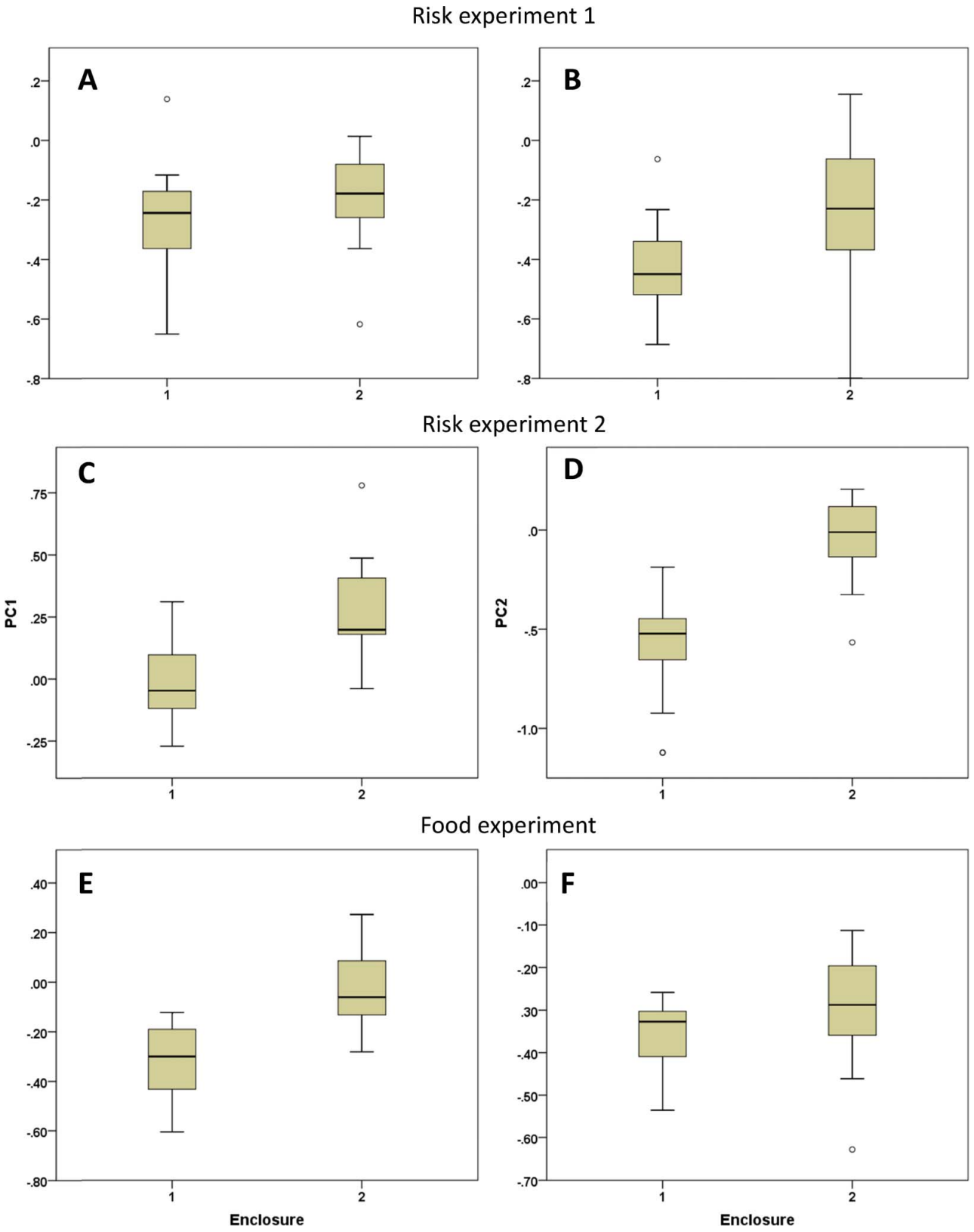

Figure 4. Patterns of habitat preference exhibited by groups of meadow voles with different personality trait scores when given a choice between two enclosures in experiments conducted in northern Ontario, Canada. Left panels refer to PC1, and those on the right to PC2.

Discussion

Experiments varying the spatial scale of risky versus safe foraging sites revealed clear patterns in both activity density and GUDs. Those patterns confirmed five of seven *a priori* predictions. Voles visited risky trays and habitats less often than safe sites and also harvested fewer resources from risky trays than they did from safe ones, regardless of scale. But voles also expressed a bias in habitat use

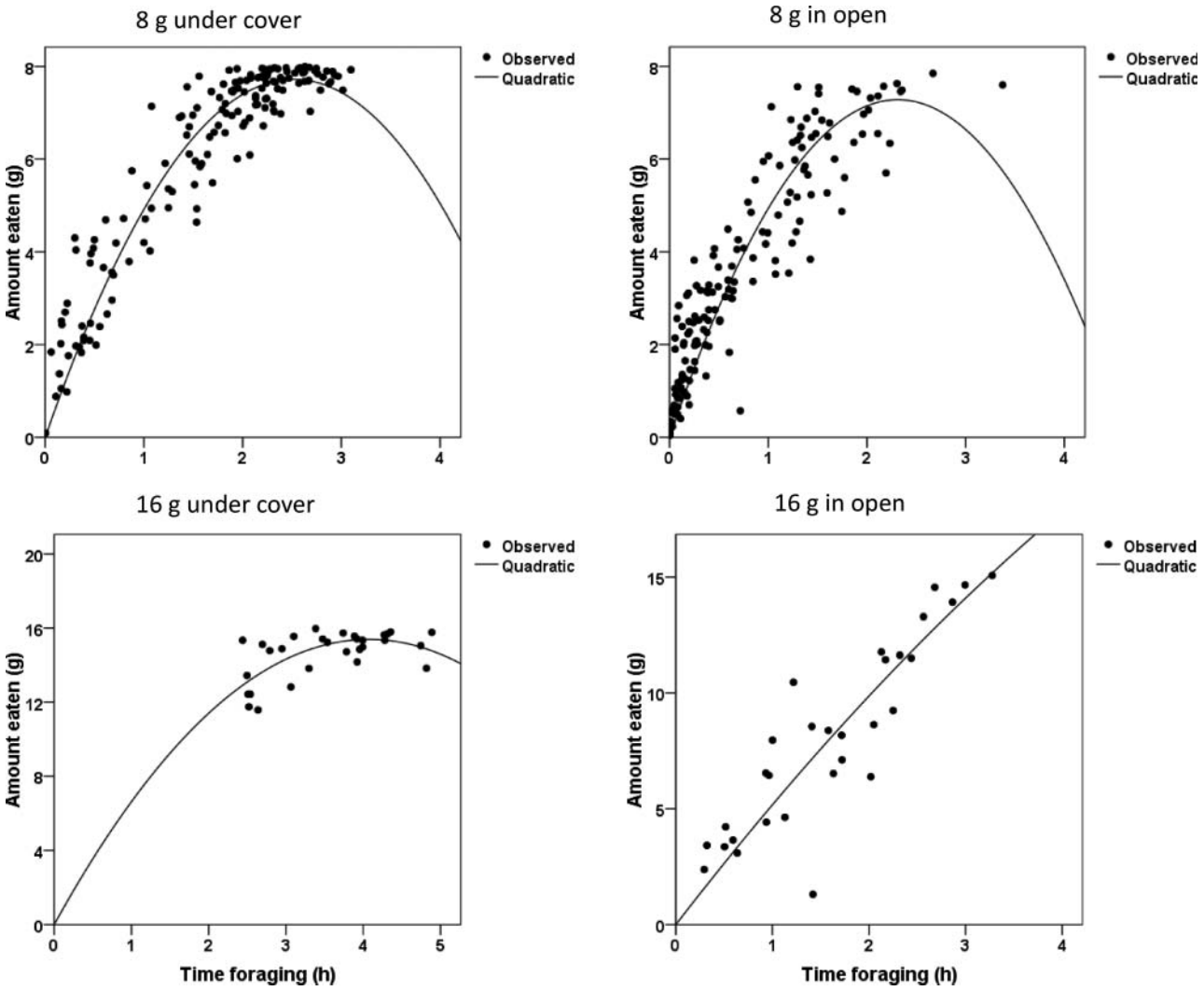

Figure 5. Harvest curves (mass of whole oats consumed vs. time) of meadow voles foraging in covered and open foraging patches containing different initial food densities.

(preference for enclosure 1 over 2) over and above that expected by manipulations of safety and habitat richness. That bias also failed to correspond exactly with patterns in GUDs. The preference for enclosure 1 was, however, linked to groups of voles that differed in temperament. But those scores were not associated with three easily differentiated foraging classes.

These results reveal strategies that adjust the use of space and foraging opportunities to reflect the spatial patchiness of the environment. Even so, animals use those strategies in somewhat complex ways that fail to yield perfect correspondence between patterns of activity density and space use with patterns of resource harvest. They thereby alert us not to expect perfect correspondence between temperament traits with foraging repertoires and the use of space under risk of predation. To what degree does the lack of complete correspondence inform us about adaptive decisions that animals might make and the emergent outcomes on populations and evolution?

We can gain some insight by re-examining the harvest curves. If activity density alone determines resource harvest, there is little reason to suspect differences in rates of resource procurement among different patch types. Animals would adjust their visitation rates to match the risks and rewards associated with each patch. This is clearly not the case for voles where rather large differences in patch residence time, and most especially under cover, emerge for similar rates of visitation. Voles visit safe patches frequently, but cumulate vastly different periods of foraging time. Voles visit risky patches less often and with far less variance in cumulative time. These differences in behaviour suggest sophisticated strategies of risk management (Brown & Kotler 2004). Voles foraging under risk focus their attention towards maximizing rates of resource harvest while minimizing the amount of time spent in heightened susceptibility to predation. The same voles feeding under safety forage somewhat more "casually".

Two reasonable hypotheses can account for the different foraging behaviours of voles when feeding under risk versus safety. (1) Intense foraging is energetically expensive or is otherwise inefficient. Although maximum foraging speed is necessary to minimize risk, it yields a relatively lower energy gain than does slower and more thorough foraging. It should be used only when the risk is high. (2) Given the opportunity to forage more safely,

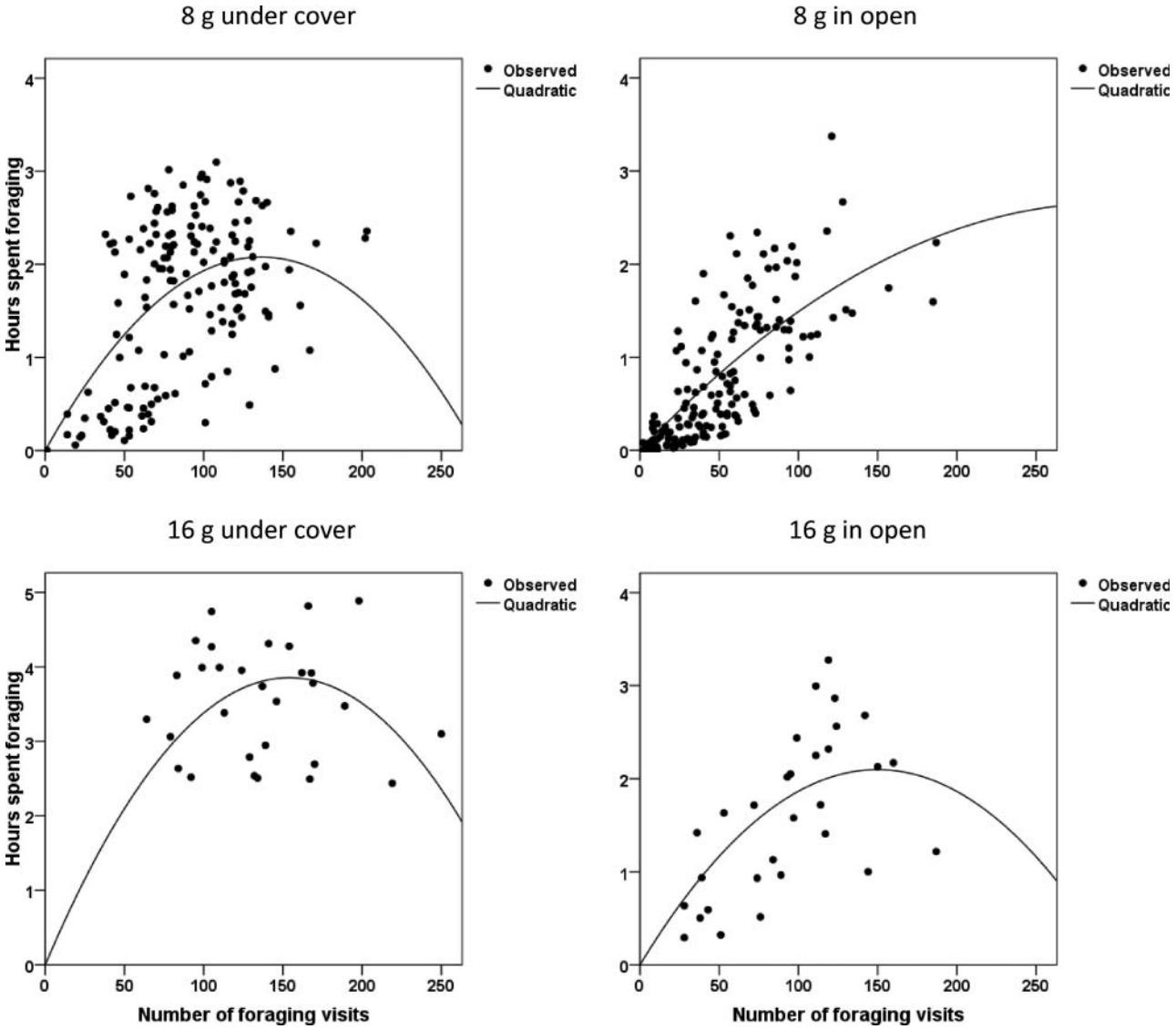

Figure 6. Quadratic regressions (lines) summarizing the cumulative amount of time that voles spent in artificial foraging trays for differing numbers of total foraging visits to those trays.

animals optimize foraging behaviour in the context of alternative fitness-enhancing activities (such as resting, grooming, and digesting food). Foraging is less intense because voles gain fitness from competing activities.

Regardless of which hypothesis might best account for differences in vole foraging behaviour, it is clear that the animals recognize risk and opportunity at different scales and adjust their behaviours accordingly. Voles prefer safe versus risky sites at both the patch and habitat scale. At the scale of individual foraging stations, voles choose safety over danger, but they are more prone to do so in rich versus poor habitats. These varying habitat and patch preferences convey intriguing insights to anyone contemplating hierarchical habitat selection. There can be little doubt that different patterns of habitat use emerge at geographical ranges, home ranges, and patch scales (first- through third-order selection, Johnson 1980). Those patterns emerge from scale dependence in processes such as foraging and dispersal, but the processes need not represent a lock-step hierarchy from one scale to another.

Differences in mean temperament between enclosures provide a tantalizing glimpse of habitat's potential role in sympatric speciation. Competitive speciation (Rosenzweig 1978, 1995) for sexually reproducing species is possible only if different types of individuals tend to occupy different ecological opportunities (also referred to as phenotype-dependent habitat choice, Bolnick et al. 2009), and if those individuals engage in assortative mating. Biased habitat occupancy and reduced gene flow in combination with potential divergence through mutation can, with sufficient time, produce the necessary (but not necessarily sufficient) divergence and reproductive isolation required for species formation (Bolnick et al. 2009). Putative mammalian examples include cryptic pelage polymorphisms in various taxa. These polymorphisms are most notable in *Peromyscus* species where they reduce predation rates and yield sharp discontinuities in association with habitat (Vignieri et al. 2010; Linnen et al. 2013). Divergence in such systems is reinforced because the mismatch of fur colouration with substrate imposes a rather

substantial survival cost among individuals that switch from one habitat to another (Nosil 2012).

Mismatches of habitat with body size, shape, and trophic morphology also appear to account for sharp gradients of character displacement between limnetic and benthic morphotypes that typify numerous species of freshwater fishes. Ecological speciation in these taxa is suggested by assortative mating and maintenance of morphological differences in the face of gene flow (Schluter 1996). Despite conflicting evidence of substantial habitat-dependent phenotypic plasticity (Robinson & Parsons 2002), adaptive behaviours of many fish species, and most particularly mate choice, are often associated with habitat (Scordato et al. 2014). Behaviour thus functions to create and maintain divergence in traits (Seehausen et al. 1997) that can lead to frequency-dependent sympatric speciation (van Doorn et al. 2004). One can anticipate similar mismatches involving foraging behaviour, risk assessment, mate choice, and other attributes of habitat among groups of animals differing in temperament. Whether those mismatches lead to segregated and spatially polymorphic populations will depend on spatial scale, the repeatability of behaviour, and the mode and degree to which behaviour is inherited (or not).

Although behavioural differences among voles using different habitats are suggestive of a potential role in insipient spatial segregation, there is no current evidence that they are associated with either of Nosil's (2012) "cost of switching habitats" or "differences between habitats in foraging efficiency" mechanisms that enhance ecological speciation. Groups of animals with different mean PC scores were not obviously associated with experimentally induced habitat differences in predation risk and food abundance, or with groups demonstrating clear differences in foraging strategies. Even if the apparent habitat segregation among groups with different mean scores is adaptive, it would appear of rather small effect, but an effect that cannot be ignored.

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